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SWIMBLADDER ALLOMETRY OF SELECTED MIDWATER FISH SPECIES

Albert L. Brooks

Naval Underwater Systems Center
New London, Connecticut

5 January 1976

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Volume of Swimbladders

20. ABSTRACT (Continue on reverse side if necessary and identify by block number)

This study examines the relationship of fish standard length to swimbladder length, width, and volume. The intra- and inter-specific variation is studied in over 1600 selected mesopelagic fish specimens belonging to 55 species from 9 families. These species are believed to account for most of the volume reverberation occurring throughout a large part of the Sargasso Sea.

Regression equations presented in this report allow calculation of swimbladder volumes directly from measurements of fish standard length for 55 species of midwater

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20. (Cont'd)

fish. Additional equations allow the calculation of swimbladder length and width from measurements of the standard lengths of these same species. It is shown that for 40 species, bladder volume increases with increasing standard length. Slopes of the regression lines for 14 species are shown to be insignificant from zero. For one species, bladder volume decreases slightly with increasing standard length.

Volume of the swimbladder of a given species of given standard length can vary greatly as can the elevations and slopes of the regression lines for different fish species.

Analyses of data for 20 fish species suggest that the actual formation of the swimbladder occurs during the late larval-early postlarval stage of development.

Two-thirds of the fish species on which this study is based are not included in previously published studies of swimbladder allometry. In publications where comparison of common species is possible, swimbladder volumes reported here are in general agreement with measurements published by N. B. Marshall but are less than volumes estimates by other authors.

The overall mean ratios for swimbladder equivalent spherical radii as a percentage of fish minimum, maximum, and mean standard lengths are 3.0, 4.2, and 3.5 percent, respectively.

Results of this study demonstrate that equations currently in use overestimate the volumes of the swimbladders and thus acoustic cross sections of many midwater fish species.

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PREFACE

This report was prepared under NUSC Project No. A-626-02, "Biological Reverberation Affecting Sonar Performance/Design," Principal Investigator, C. L. Brown (Code TA13), and Navy Subproject and Task No. SF 525 526 01-19325, Program Manager, A. Franceschetti (Naval Sea Systems Command, Code SEA-06H1).

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R. W. Hasse
Associate Director for Sonar Research

The author of this report is located at the New London Laboratory, Naval Underwater Systems Center, New London, Connecticut 06320.

SWIMBLADDER ALLOMETRY OF SELECTED MIDWATER FISH SPECIES

INTRODUCTION

Since the discovery by Eyring et al. in 1942 of a deep layer in the ocean that scattered sound, a voluminous literature has been written dealing with the acoustics and biology of what is now called the Deep Scattering Layer (DSL). Many theoretical, field, and laboratory studies [Hersey and Backus (1962), Eyring, Christensen, and Raitt (1948), Marshall (1951), Dietz (1948), Andreeva and Chindonova (1964), Batzler and Pickwell (1970), Chapman and Marshall (1966), Haslett (1962), Smith (1954), Moore (1948), and Barham (1957)] have been done to determine the organisms and mechanisms responsible for biological scattering of underwater sound. Though organisms such as siphonophores, euphausiids, and cephalopods have, in some cases, been implicated as the cause of sonic scattering layers, overwhelming evidence indicates that volume reverberation in the open ocean is largely due (as first suggested by Marshall (1951)) to gas-filled cavities (principally swimbladders) of small mesopelagic (midwater) fish.

Despite this, only limited quantitative information exists relating swimbladder characteristics to scattering. More fundamentally, very few data are available on the relationships between bladder dimensions — length, width, and volume — and fish morphometry. The most extensive study of the swimbladders of deep-sea fish was reported by Marshall (1951, 1960, 1972). More recently, Shearer (1970) has measured swimbladder volumes of four species of mesopelagic fishes, some dipnetted at the surface and others caught in a midwater trawl; Capen (1967) studied the morphology of the swimbladders of some mesopelagic fishes in relation to sound scattering; and Kleckner and Gibbs (1972), in a survey of swimbladder structure, reported the presence of swimbladders in 23 of 32 examined species of midwater fishes collected from the Mediterranean. Butler and Pearcy (1972) reported on swimbladder morphology of northeastern Pacific myctophids.

This report examines the relationship of fish standard length to swimbladder length, width, and volume. Also studied are the intra- and inter-specific allometric variations encountered in these variables in over 1600 selected mesopelagic specimens belonging to 55 species from 9 families. These fish repre-

sent the predominant bladdered species believed to account for most volume reverberation occurring throughout much of the Sargasso Sea.

METHODS AND MATERIALS

Individuals used in this study were selected from over 100,000 fish specimens collected during the Ocean Acre program of research on acoustic and biological characteristics of the DSL in a 1-degree square of open ocean off Bermuda. Between 1967 and 1972, 14 cruises were made to the Ocean Acre area. During these cruises, 317 Isaacs-Kidd Midwater Trawl (IKMT) tows yielded 538 discrete-depth and 300 nondiscrete-depth samples over depths ranging from the surface to 2500 meters. Engel Midwater Trawl (EMT) tows yielded an additional 48 nondiscrete-depth samples. Also included in this study are fish specimens collected during August-October, 1970, from the Mediterranean Sea (Gibbs et al., 1972). Measurements of fish standard length and swimbladder dimensions of 541 of these individuals in 11 species belonging to 3 families were kindly loaned to the author by R. C. Kleckner. These 11 species, plus others, were the subject of an earlier report on swimbladder structure of Mediterranean midwater fishes by Kleckner and Gibbs (1972) and also the subject of an M.S. dissertation by Kleckner (1974). Regression formulas presented in these reports relate fish standard length to swimbladder length and width, which allows subsequent calculation of swimbladder volume. These data are used here to more directly relate standard length to swimbladder volume by means of a data transformation. Conclusions about morphometric relationships are assumed to hold true for like species collected from the Ocean Acre.

All fish were preserved in 10-percent sea water formalin after retrieval of each tow. In the laboratory, specimens were washed and transferred through a series of increasingly concentrated solutions of ethanol up to 70 percent. Standard length (snout tip to caudal base) was measured in millimeters with dial calipers. Dissections to reveal the swimbladders were made under a microscope; measurements of bladder length (the anterior-posterior length of the external swimbladder wall) and bladder width (the greatest width of the bladder wall) were made with an ocular micrometer.

The swimbladder volume V of each specimen was calculated using the formula for a prolate spheroid,

$$V = (4/3)\pi ab^2 , \tag{1}$$

where a is the semi-major axis and b is the semi-minor axis.

Many investigators, located at the Smithsonian Institution, where the specimens are deposited, and at the University of Rhode Island, contributed to the species identification and measurement of specimens and bladders. Both organizations participated in the Ocean Acre program.

For a detailed discussion of the Ocean Acre field study methods as well as a geographic, hydrographic, acoustic, and physico-chemical description of the study area and summary of the biology, the reader is referred to Brown and Brooks (1974) and Brooks (1972). Other accounts dealing with laboratory methods, vertical distribution, ecology, and life histories of specific taxa collected may be found in Bond (1974), Gibbs and Roper (1970), Gibbs (1971), Gibbs et al. (1971A and B), Goodyear and Gibbs (1970), Keene (1970), Krueger and Bond (1972), Roper et al. (1970), Kleckner (1974), and Donaldson (1973).

RESULTS AND DISCUSSION

REGRESSION ANALYSES — FISH STANDARD LENGTH VERSUS SWIMBLADDER LENGTH AND WIDTH

Table 1 lists the 55 species of air-bladdered mesopelagic fishes studied. Though all of these species occur in the Ocean Acre region, data for the 11 species marked with an asterisk were obtained from fish collected from the Mediterranean. Preliminary plots showed that the relationship between fish standard lengths and their respective swimbladder lengths and widths was approximately linear (also shown by Kleckner and Gibbs, 1972). To determine the precise nature of this relationship, the measurement data were subjected to a linear regression analysis by the method of least squares (Skory and Jennings, 1969).

Table 2 presents some of the results of these analyses. All measurements in the table are in millimeters. The left-hand section of the table lists alphabetically the mesopelagic fish species, total number of specimens, range of standard lengths, and the mean standard length $\overline{L}_{STD}$ of individuals included in the analysis. The center section lists the mean of the swimbladder lengths $\overline{L}_{SB}$, the regression equations relating swimbladder length L_{SB} to fish standard length L_{STD}, and the correlation coefficients R. An F test (Snedecor, 1956, p. 244) was performed to examine the significance of the slope of the regression lines. An asterisk preceding a regression equation indicates that at the 0.05 probability level, the slope of that line was not significantly different from zero. The right-hand section of the table lists the mean of the swimbladder widths $\overline{W}_{SB}$, the regression equations relating swimbladder width W_{SB} to fish standard length

Table 1. Predominant Bladdered Species According to Family

Myctophidae	Gonostomatidae
Benthosema suborbitale	Bonapartia pedaliota
Bolinichthys indicus	*Ichthyococcus ovatus
Bolinichthys photothorax	Pollichthys mauli
*Ceratoscopelus maderensis	Valenciennellus tripunctulatus
Ceratoscopelus warmingi	*Vinciguerria attenuata
Diaphus brachycephalus	*Vinciguerria poweriae
Diaphus metapoclampus	
Diaphus mollis	**Sternoptychidae**
Diaphus problematicus	
*Diaphus rafinesquei	Argyropelecus aculeatus
Diogenichthys atlanticus	*Argyropelecus hemigymnus
*Hygophum benoiti	Sternoptyx diaphana
*Hygophum hygomi	
Hygophum taaningi	**Melamphaidae**
Lampadena chavesi	
Lampadena luminosa	Melamphaes pumilus
Lampadena speculigera	Melamphaes typhlops
Lampadena urophaos	Scopeloberyx opisthopterus
Lampanyctus alatus	
Lampanyctus ater	**Berycidae**
*Lampanyctus crocodilus	
Lampanyctus cuprarius	Anoplogaster cornuta
Lampanyctus festivus	Poromitra capito
Lampanyctus lineatus	
Lampanyctus photonotus	**Bregmacerotidae**
*Lampanyctus pusillus	
Lepidophanes gaussi	Bregmaceros sp.
Lepidophanes guentheri	
*Lobianchia dofleini	**Melanostomiatidae**
Lobianchia gemellari	
Myctophum nitidulum	Melanostomiatid larvae
Notolychnus valdiviae	
Notoscopelus caudispinosus	**Nomeidae**
Notoscopelus resplendens	
Symbolophorus rufinus	Cubiceps sp.
Taaningichthys bathyphilus	
Taaningichthys minimus	**Opisthoproctidae**
	Rhynchohyalus natalensis

Table 2. Regression Analysis of Swimbladder Length and Width on Standard Length

Species	Number of Specimens	Range of STD Lengths	Mean of STD Length L_{STD}	Mean of Swimbladder Length $\bar{L}_{SB}$	Regression Equation L_{SB} on L_{STD}	Correl. Coeff. R	Mean of Swimbladder Width $\bar{W}_{SB}$	Regression Equation W_{SB} on L_{STD}	Correl. Coeff. R
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	* $1.379+0.038L_{STD}$	0.85	[illegible]	$0.755+0.022L_{STD}$	0.97
Argyropelecus aculeatus	[illegible]	9.0-55.9	[illegible]	[illegible]	$-0.301+0.150L_{STD}$	0.98	[illegible]	$0.069+0.073L_{STD}$	0.91
Argyropelecus hemigymnus	[illegible]	7.2-33.8	[illegible]	2.7	$-0.421+0.156L_{STD}$	0.97	[illegible]	$-0.253+0.094L_{STD}$	0.96
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	$-2.375+0.319L_{STD}$	0.84	[illegible]	$-0.607+0.081L_{STD}$	0.65
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	$1.575+0.153L_{STD}$	0.46	[illegible]	$-0.114+0.045L_{STD}$	0.50
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	* $0.376+0.208L_{STD}$	0.60	[illegible]	* $-0.140+0.050L_{STD}$	0.42
Bonapartia pedaliota	[illegible]	[illegible]	[illegible]	[illegible]	$-3.147+0.240L_{STD}$	0.88	[illegible]	$-0.516+0.059L_{STD}$	0.74
[illegible] sp.	[illegible]	[illegible]	[illegible]	[illegible]	* $2.267+0.032L_{STD}$	0.58	[illegible]	* $0.410+0.013L_{STD}$	0.51
Ceratoscopelus maderensis	[illegible]	7.4-75.3	[illegible]	[illegible]	$0.879+0.084L_{STD}$	0.85	[illegible]	$0.462+0.023L_{STD}$	0.5[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	$1.532+0.074L_{STD}$	0.53	[illegible]	$0.653+0.014L_{STD}$	0.43
[illegible] sp.	[illegible]	[illegible]	[illegible]	[illegible]	$3.848+0.104L_{STD}$	0.90	[illegible]	* $1.924-0.001L_{STD}$	0.03
Diaphus brachycephalus	[illegible]	[illegible]	[illegible]	[illegible]	* $2.738+0.134L_{STD}$	0.20	[illegible]	* $3.286-0.046L_{STD}$	0.26
Diaphus metopoclampus	[illegible]	[illegible]	[illegible]	[illegible]	$-1.540+0.262L_{STD}$	0.89	[illegible]	$-0.769+0.078L_{STD}$	0.74
Diaphus mollis	[illegible]	[illegible]	[illegible]	[illegible]	$3.779+0.103L_{STD}$	0.45	[illegible]	* $0.893+0.004L_{STD}$	0.06
Diaphus problematicus	[illegible]	[illegible]	[illegible]	[illegible]	* $7.581+0.012L_{STD}$	0.07	[illegible]	* $2.565-0.016L_{STD}$	0.33

Table 2. (Cont'd) Regression Analysis of Swimbladder Length and Width on Standard Length

Species	Number of Specimens	Range of STD Lengths	Mean of STD Length $\bar{L}_{STD}$	Mean of Swimbladder Length $\bar{L}_{SB}$	Regression Equation L_{SB} on L_{STD}	Correl. Coeff. R	Mean of Swimbladder Width $\bar{W}_{SB}$	Regression Equation W_{SB} on L_{STD}	Correl. Coeff. R
Diaphus rafinesquei	49	7.4-77.6	[illegible]	[illegible]	$-1.486+0.240L_{STD}$	0.95	[illegible]	$-1.256+0.089L_{STD}$	0.87
Diogenichthys atlanticus	[illegible]	11.1-19.4	[illegible]	[illegible]	$-1.559+0.259L_{STD}$	0.84	[illegible]	$-0.439+0.075L_{STD}$	0.73
Hygophum benoiti	[illegible]	6.3-44.0	[illegible]	[illegible]	$-0.119+0.150L_{STD}$	0.81	[illegible]	$-0.005+0.050L_{STD}$	0.87
Hygophum hygomi	[illegible]	5.7-59.1	[illegible]	[illegible]	$0.447+0.119L_{STD}$	0.52	1.4	$0.085+0.035L_{STD}$	0.55
Hygophum taaningi	15	[illegible]	[illegible]	[illegible]	$0.740+0.091L_{STD}$	0.64	[illegible]	$-0.147+0.042L_{STD}$	0.71
Ichthyococcus ovatus	26	12.0-35.0	25.1	[illegible]	$-1.901+0.241L_{STD}$	0.96	[illegible]	$-0.654+0.095L_{STD}$	0.94
Lampadena chavesi	10	[illegible]-31.7	[illegible]	[illegible]	$-1.371+0.167L_{STD}$	0.85	[illegible]	$-0.845+0.059L_{STD}$	0.91
Lampadena luminosa	7	[illegible]	44.7	[illegible]	$-0.927+0.129L_{STD}$	0.96	[illegible]	* $0.638+0.007L_{STD}$	0.29
Lampadena speculigera	[illegible]	13.8-21.5	[illegible]	[illegible]	$-4.008+0.320L_{STD}$	0.85	[illegible]	* $1.667-0.041L_{STD}$	0.30
Lampadena urophaos	[illegible]	[illegible]	49.3	[illegible]	$-0.474+0.132L_{STD}$	0.76	1.7	$-0.204+0.037L_{STD}$	0.60
Lampanyctus alatus	11	30.3-51.2	39.3	[illegible]	* $0.999+0.123L_{STD}$	0.55	[illegible]	$-0.908+0.055L_{STD}$	0.61
Lampanyctus ater	[illegible]	[illegible]	[illegible]	[illegible]	$2.364-0.018L_{STD}$	[illegible]	[illegible]	$0.854-0.004L_{STD}$	0.34
Lampanyctus crocodilus	[illegible]	9.5-171.7	[illegible]	[illegible]	$-2.642+0.191L_{STD}$	[illegible]	[illegible]	$-0.397+0.042L_{STD}$	0.92
Lampanyctus cuprarius	47	[illegible]-87.1	[illegible]	[illegible]	* $1.026-0.003L_{STD}$	0.12	[illegible]	$0.604-0.004L_{STD}$	0.41
Lampanyctus festivus	37	[illegible]	[illegible]	[illegible]	$-0.717+0.135L_{STD}$	0.85	[illegible]	$-0.163+0.035L_{STD}$	0.69

Table 2. (Cont'd) Regression Analysis of Swimbladder Length and Width on Standard Length

Species	Number of Specimens	Range of STD Lengths	Mean of STD Length $\bar{L}_{STD}$	Mean of Swimbladder Length $\bar{L}_{SB}$	Regression Equation L_{SB} on L_{STD}	Correl. Coeff. R	Mean of Swimbladder Width $\bar{W}_{SB}$	Regression Equation W_{SB} on L_{STD}	Correl. Coeff. R
Lampanyctus lineatus	11	36.3-121.9	79.9	1.[illegible]	* $1.991-0.009L_{STD}$	0.34	0.6	* $0.652-0.001L_{STD}$	0.20
Lampanyctus photonotus	43	21.3-64.3	41.5	[illegible].1	$0.036+0.145L_{STD}$	0.81	1.3	$0.214+0.027L_{STD}$	0.52
Lampanyctus pusillus	48	6.4-40.0	27.3	4.0	$-0.760+0.172L_{STD}$	0.92	1.0	$0.061+0.034L_{STD}$	0.79
Lepidophanes gaussi	32	15.4-41.9	28.[illegible]	4.[illegible]	$-1.924+0.235L_{STD}$	0.87	1.0	$-0.169+0.039L_{STD}$	0.54
Lepidophanes guentheri	6	16.4-[illegible]	40.[illegible]	7.2	$-1.370+0.213L_{STD}$	0.95	1.4	$-0.033+0.036L_{STD}$	0.97
Lobianchia dofleini	58	12.0-42.4	25.9	3.3	$0.327+0.116L_{STD}$	0.56	1.0	$0.146+0.033L_{STD}$	0.50
Lobianchia gemellari	42	12.8-99.8	29.7	5.7	$-2.462+0.276L_{STD}$	0.97	[illegible]	$-0.003+0.040L_{STD}$	0.88
Melamphaes pumilus	59	10.2-21.4	17.8	[illegible].0	$-1.660+0.208L_{STD}$	0.83	1.[illegible]	$-0.402+0.081L_{STD}$	0.77
Melamphaes typhlops	30	9.6-70.8	3[illegible].5	5.1	$-1.916+0.192L_{STD}$	0.89	2.3	$-0.435+0.074L_{STD}$	0.89
[illegible] stoniatii Larvae	8	11.0-16.0	13.7	1.1	$-1.044+0.154L_{STD}$	0.89	0.5	* $-0.174+0.051L_{STD}$	0.51
Myctophum nitidulum	21	16.[illegible]-63.0	27.5	3.[illegible]	$-2.087+0.205L_{STD}$	0.97	1.2	$-0.413+0.059L_{STD}$	0.90
Notolychnus valdiviae	34	14.6-21.7	18.9	2.0	* $2.442-0.022L_{STD}$	0.10	0.8	* $-0.133+0.047L_{STD}$	0.32
Notoscopelus caudispinosus	6	41.5-67.3	55.2	7.1	* $3.403+0.068L_{STD}$	0.41	1.7	* $1.638+0.001L_{STD}$	0.04
Notoscopelus resplendens	60	21.7-72.6	40.1	4.5	$0.897+0.089L_{STD}$	0.70	1.0	$0.584+0.010L_{STD}$	0.37
Pollichthys mauli	3[illegible]	31.0-48.[illegible]	39.8	[illegible]	* $3.037+0.013L_{STD}$	0.08	1.5	* $0.315+0.030L_{STD}$	0.32

Table 2. (Cont'd) Regression Analysis of Swimbladder Length and Width on Standard Length

Species	Number of Specimens	Range of STD Lengths	Mean of STD Length $\bar{L}_{STD}$	Mean of Swimbladder Length $\bar{L}_{SB}$	Regression Equation L_{SB} on L_{STD}	Correl. Coeff. R	Mean of Swimbladder Width $\bar{W}_{SB}$	Regression Equation W_{SB} on L_{STD}	Correl. Coeff. R
Peromitra capito	[illegible]	[illegible]	[illegible]	[illegible]	$-1.839+0.158L_{STD}$	0.95	[illegible]	$-0.605+0.073L_{STD}$	0.92
Rhynchohyalus natalensis	[illegible]	[illegible]	[illegible]	[illegible]	$-3.882+0.308L_{STD}$	0.99	[illegible]	* $0.429+0.022L_{STD}$	0.63
Scopeloberyx opisthopterus	[illegible]	[illegible]	[illegible]	[illegible]	$0.820+0.069L_{STD}$	0.69	[illegible]	$-0.392+0.071L_{STD}$	0.83
Sternoptyx diaphana	30	8.9-35.0	[illegible]	[illegible]	$-0.853+0.204L_{STD}$	0.90	[illegible]	$-0.483+0.115L_{STD}$	0.93
Symbolophorus rufinus	[illegible]	[illegible]	[illegible]	[illegible]	$-1.709+0.165L_{STD}$	0.82	[illegible]	$-0.336+0.040L_{STD}$	0.74
Taaningichthys bathyphilus	25	[illegible]	[illegible]	5.3	$-0.829+0.146L_{STD}$	0.94	2.5	$-0.391+0.060L_{STD}$	0.79
Taaningichthys minimus	[illegible]	[illegible]	[illegible]	[illegible]	$-[illegible].603+0.251L_{STD}$	0.88	[illegible]	$-1.045+0.068L_{STD}$	0.71
Valenciennellus tripunctulatus	[illegible]	[illegible]	[illegible]	[illegible]	$-0.243+0.166L_{STD}$	0.87	[illegible]	$-0.266+0.076L_{STD}$	0.70
Vinciguerria attenuata	44	[illegible]	[illegible]	[illegible]	$-1.057+0.177L_{STD}$	0.97	[illegible]	$-0.115+0.043L_{STD}$	0.80
Vinciguerria poweriae	34	[illegible]	[illegible]	[illegible]	$-1.253+0.186L_{STD}$	0.89	[illegible]	$-0.120+0.044L_{STD}$	0.76

*An F test indicates that the slope of these regression lines is not significant at the 0.05 level.

L_{STD}, and the corresponding correlation coefficients. As before, an asterisk indicates that the slope of the regression line is not significant at the 0.05 level of probability. Note that for some species the sample size is small (e.g., for 9 of the species listed, measurement data were available for fewer than 10 specimens). Although the precision of the regression analyses in these cases may be reduced, they are included here because of the absence in the literature of this type of information.

Sample correlation coefficients R between swimbladder length and fish standard length equal or exceed 0.70 in 37 of the 55 species. The R values between swimbladder width and fish standard length are not as high, with 27 of the 55 species exceeding a value of 0.70. The F test (0.05 level) indicates that there is no significant relationship in 11 species between standard length and bladder length. Also, no significant relationship between fish standard length and bladder width is found for 14 species. In most, though not all, of these cases, a nonsignificant slope is associated with a small sample size. Inspection of a plot of standard lengths against bladder lengths and widths suggests that, if more data were included in the analysis, a significant slope would result for several species.

For those species where a significant slope is found, it is positive (i.e., bladder length or width or both increase with increasing standard length)* for all species except Lampanyctus ater and L. cuprarius, whose slopes are slightly negative.

REGRESSION ANALYSES — FISH STANDARD LENGTH VERSUS SWIMBLADDER VOLUME

Measurements of the swimbladder lengths and widths of the same specimens used in the previous analyses were converted to volumes using equation (1). Arithmetic plots of standard length against swimbladder volumes of four species representing the four most important fish families found in the Ocean Acre are shown in figure 1A-D. A line of best fit, drawn by eye through the scatter of points, clearly shows for each species a nonlinear relationship between these variables. Any linear regression analysis of these data in raw form would yield unacceptable errors. On the other hand, curvilinear analysis of these data becomes burdensome and complicated.

*Increasing standard length is also a measure of increasing age, growth, or both.

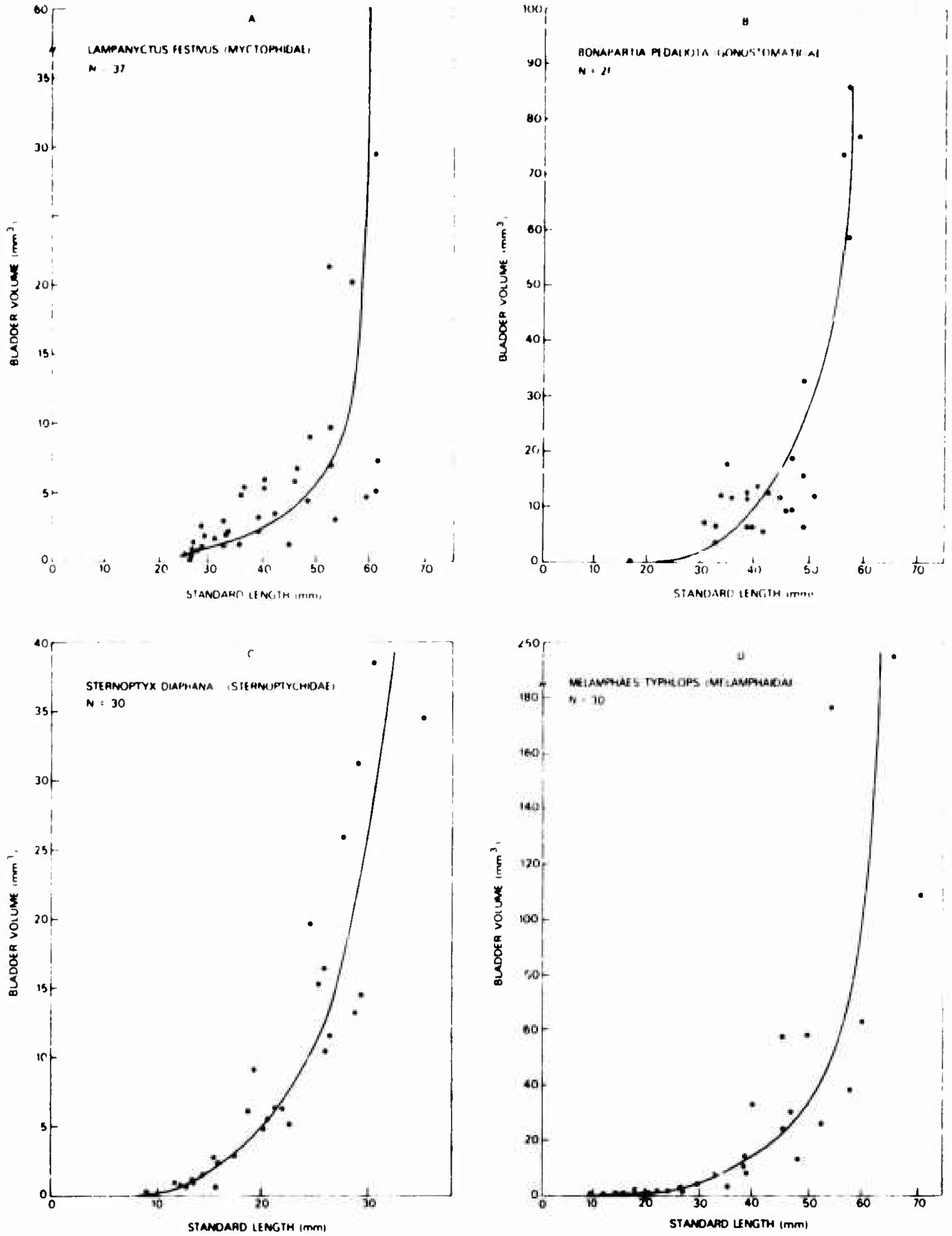

Figure 1. Arithmetic Plots of Swimbladder Volume Against Fish Standard Length for Representatives of Four Important Midwater Fish Families

To overcome these problems, the dependent variable (bladder volume) was transformed to a new scale of measurement. The practice of transforming raw data, especially marine biological data, as discussed by Barnes, 1962; Barnes and Bagenal, 1951; Silliman, 1946; and Winsor and Clarke, 1940, often succeeds in achieving multiple benefits to the subsequent statistical treatment of the data (Steel and Torrie, 1960). Logarithmic transformations of various types have been applied to fisheries data similar to the present data. Preliminary treatment of measurements provided by Kleckner on 11 species of Mediterranean midwater fishes indicated that a logarithmic transformation succeeded well in satisfying the assumptions underlying the regression technique and the analysis of variance.

Table 3 lists the means, variances, and standard deviations (0.05 probability level) resulting from the regression analysis of fish standard length against the untransformed and transformed swimbladder volumes V_{SB} and demonstrates the ability of the log $(V_{SB} + 1)$ transformation (1) to stabilize the variance and thus more closely approach a normal distribution of residuals, and (2) to drastically reduce the proportionality observed between the untransformed means and their corresponding standard deviations. The mean values listed under the column headed Transformed Bladder Volumes are what Barnes (1952) calls "derived" means. They are calculated by adding 1.15 times the variance to the transformed mean before transforming back to the original scale of measurement. The author submits that, with the possible exception of Lampanyctus crocodilus, these derived means estimate the actual means with reasonable efficiency.

On the basis of the foregoing, the calculated values for swimbladder volumes V_{SB} were transformed to log $(V_{SB} + 1)$ and regressed against measurements of standard length. A digest of the results of these analyses is presented in table 4. The first four columns are the same as found in table 2, because the same individuals were used in each analysis. The fifth column lists the derived mean in cubic millimeters of all the swimbladder volumes $\overline{V}_{SB}$ used in the analysis of a given species. The regression equation for each species (column 6) relating the transformed swimbladder volumes to standard length is in the following form:

$$\log (V_{SB} + 1) = a + bL_{STD} \quad , \qquad (2)$$

Table 3. Untransformed Versus Transformed Swimbladder Volume Data

Species	N	Mean Untransformed Bladder Volumes	Mean Transformed Bladder Volumes	Variance Untransformed Data	Variance Transformed Data	Standard Deviation Untransformed Data	Standard Deviation Transformed Data
Argyropelecus hemigymnus	47	5.79	6.16	36.1	0.2	6.0	0.4
Ceratoscopelus maderensis	45	6.86	6.12	198.6	0.2	14.1	0.5
Diaphus rafinesquei	49	97.49	116.94	21977.9	0.4	148.3	0.6
Hygophum benoiti	70	4.33	3.75	63.4	0.2	8.0	0.5
Hygophum hygomi	55	11.07	9.18	831.6	0.2	28.8	0.5
Ichthyococcus ovatus	26	10.36	12.76	81.2	0.3	9.0	0.5
Lampanyctus crocodilus	65	85.15	65.66	79332.3	0.7	281.7	0.9
Lampanyctus pusillus	48	2.83	2.75	25.1	0.1	5.0	0.3
Lobianchia dofleini	58	2.73	2.52	6.2	0.1	2.5	0.3
Vinciquerria attenuata	44	1.36	1.29	3.7	0.1	1.9	0.3
Vinciquerria poweriae	34	1.31	1.29	2.3	0.1	1.5	0.2

Table 4. Regression Analysis of Swimbladder Volume on Standard Length

Species	Number of Specimens	Range of STD Lengths	Mean of STD Length $\bar{L}_{STD}$	Derived Mean of Swimbladder Volumes $\bar{V}_{SB}$	Regression Equation $\text{Log}(V_{SB}+1)=a+bL_{STD}$	Correl. Coeff. R
Anoplogaster cornuta	5	11.5-81.5	37.6	5.6	$0.139+0.013L_{STD}$	0.97
Argyropelecus aculeatus	30	9.0-55.9	17.1	3.6	$-0.231+0.041L_{STD}$	0.92
Argyropelecus hemigymnus	47	7.2-33.8	20.1	6.2	$-0.436+0.054L_{STD}$	0.97
Benthosema suborbitale	11	11.6-26.0	20.4	4.5	$-0.654+0.057L_{STD}$	0.71
Bolinichthys indicus	31	18.3-39.4	27.6	4.7	$-0.286+0.034L_{STD}$	0.55
Bolinichthys photothorax	10	34.6-60.6	49.2	39.7	* $0.382+0.021L_{STD}$	0.44
Bonapartia pedaliota	26	17.0-59.0	42.9	20.8	$-0.371+0.035L_{STD}$	0.83
Bregmaceros sp.	4	31.2-85.0	57.8	4.6	* $0.043+0.009L_{STD}$	0.54
Ceratoscopelus maderensis	45	7.4-75.3	35.4	6.1	$0.041+0.016L_{STD}$	0.69
Ceratoscopelus warmingi	37	18.6-66.0	39.9	4.6	$0.125+0.012L_{STD}$	0.51
Cubiceps sp.	6	27.8-81.2	47.5	19.5	* $1.031+0.003L_{STD}$	0.21
Diaphus brachycephalus	10	29.9-42.0	35.6	14.3	* $1.579-0.015L_{STD}$	0.14
Diaphus metapoclampus	11	24.5-74.6	61.6	285.3	$-0.051+0.033L_{STD}$	0.90
Diaphus mollis	20	22.1-47.2	36.1	4.9	* $0.434+0.007L_{STD}$	0.16
Diaphus problematicus	14	32.0-79.5	61.6	13.0	* $1.419-0.007L_{STD}$	0.24
Diaphus rafinesquei	49	7.4-77.6	50.0	116.9	$-0.102+0.035L_{STD}$	0.94
Diogenichthys atlanticus	32	11.1-19.4	14.3	0.6	$-0.567+0.052L_{STD}$	0.82

Table 4. (Cont'd) Regression Analysis of Swimbladder Volume on Standard Length

Species	Number of Specimens	Range of STD Lengths	Mean of STD Length $\bar{L}_{STD}$	Derived Mean of Swimbladder Volumes $\bar{V}_{SB}$	Regression Equation $Log(V_{SB}+1)=a+bL_{STD}$	Correl. Coeff. R
Hygophum benoiti	70	6.3-44.0	20.8	3.8	$-0.248+0.033L_{STD}$	0.87
Hygophum hygomi	55	5.7-59.1	38.2	9.2	$-0.042+0.021L_{STD}$	0.56
Hygophum taaningi	15	12.4-39.8	22.5	1.7	$-0.297+0.027L_{STD}$	0.72
Ichthyococcus ovatus	26	12.0-35.0	25.1	12.8	$-0.710+0.062L_{STD}$	0.96
Lampadena chavesi	10	18.5-31.7	22.0	0.8	$-0.857+0.048L_{STD}$	0.92
Lampadena luminosa	7	13.6-61.5	44.7	3.1	* $-0.036+0.012L_{STD}$	0.66
Lampadena speculigera	6	18.8-21.5	20.6	1.0	* $0.139+0.007L_{STD}$	0.11
Lampadena urophaos	35	22.6-78.3	49.8	16.2	$-0.315+0.024L_{STD}$	0.72
Lampanyctus alatus	11	30.3-51.2	39.3	6.4	$-0.595+0.034L_{STD}$	0.63
Lampanyctus ater	35	25.2-97.4	47.2	0.4	* $0.252-0.002L_{STD}$	0.29
Lampanyctus crocodilus	65	9.5-171.7	56.1	65.7	$-0.182+0.021L_{STD}$	0.97
Lampanyctus cuprarius	47	30.3-87.1	53.4	0.1	$0.069-0.001L_{STD}$	0.31
Lampanyctus festivus	37	25.3-61.3	41.2	6.0	$-0.383+0.026L_{STD}$	0.79
Lampanyctus lineatus	11	36.3-121.9	79.9	0.3	* $0.160-0.001L_{STD}$	0.29
Lampanyctus photonotus	43	21.3-64.3	41.5	7.4	$-0.181+0.023L_{STD}$	0.68
Lampanyctus pusillus	48	6.4-40.0	27.3	2.3	$-0.314+0.029L_{STD}$	0.87
Lepidophanes gaussi	32	15.4-41.9	28.6	4.0	$-0.487+0.035L_{STD}$	0.82

Table 4. (Cont'd) Regression Analysis of Swimbladder Volume on Standard Length

Species	Number of Specimens	Range of STD Lengths	Mean of Std Length $\bar{L}_{STD}$	Derived Mean of Swimbladder Volumes $\bar{V}_{SB}$	Regression Equation $\text{Log}(V_{SB}+)=a+bL_{STD}$	Correl. Coeff. R
Lepidophanes guentheri	6	16.4-52.8	40.2	15.7	$-0.403+0.032L_{STD}$	0.97
Lobianchia dofleini	58	12.0-42.4	25.9	2.5	$-0.201+0.024L_{STD}$	0.56
Lobianchia gemellari	42	12.8-99.8	29.7	7.0	$-0.134+0.025L_{STD}$	0.93
Melamphaes pumilus	59	10.2-21.4	17.5	1.4	$-0.628+0.054L_{STD}$	0.83
Melamphaes typhlops	30	9.6-70.8	36.5	32.4	$-0.357+0.037L_{STD}$	0.93
Melanostomiatid larvae	8	11.0-16.0	13.7	0.2	$*-0.194+0.019L_{STD}$	0.62
Myctophum nitidulum	21	16.3-63.6	27.5	8.8	$-0.493+0.036L_{STD}$	0.95
Notolychnus valdiviae	34	14.6-21.7	18.9	0.7	$*-0.160+0.019L_{STD}$	0.25
Notoscopelus caudispinosus	6	41.5-67.3	55.2	11.5	$*\ 0.879+0.003L_{STD}$	0.17
Notoscopelus resplendens	60	21.7-72.6	40.1	3.6	$0.056+0.011L_{STD}$	0.54
Pollichthys mauli	35	31.0-48.0	39.8	4.6	$*\ 0.129+0.014L_{STD}$	0.30
Poromitra capito	32	12.0-99.1	35.6	27.3	$-0.398+0.032L_{STD}$	0.97
Rhynchohyalus natalensis	9	16.9-52.5	33.2	6.0	$-0.269+0.029L_{STD}$	0.85
Scopeloberyx opisthopterus	30	13.0-38.6	27.9	4.7	$-0.385+0.037L_{STD}$	0.85
Sternoptyx diaphana	30	8.9-35.0	20.6	10.2	$-0.519+0.065L_{STD}$	0.96
Symbolophorus rufinus	26	14.2-85.9	38.5	8.1	$-0.346+0.022L_{STD}$	0.76

Table 4. (Cont'd) Regression Analysis of Swimbladder Volume on Standard Length

Species	Number of Specimens	Range of STD Lengths	Mean of STD Length L_{STD}	Derived Mean of Swimbladder Volumes $\bar{V}_{SB}$	Regression Equation $\log(V_{SB}^{*}) = a + bL_{STD}$	Correl. Coeff. R
Taaningichthys bathyphilus	25	17.7-6[illegible].9	48.6	38.8	$-0.437+0.035L_{STD}$	0.92
Taaningichthys minimus	31	22.1-54.2	38.7	14.3	$-0.886+0.045L_{STD}$	0.85
Valenciennellus tripunctulatus	71	1[illegible].2-29.5	21.9	4.0	$-0.453+0.050L_{STD}$	0.78
Vinciquerria attenuata	44	12.4-36.4	20.3	1.3	$-0.390+0.033L_{STD}$	0.90
Vinciquerria poweriae	34	12.1-33.7	20.6	1.3	$-0.358+0.032L_{STD}$	0.86

where a is the log (V_{SB} + 1) intercept, b is the slope of the line (i.e., the number of units of log (V_{SB} +1) corresponding to every unit of standard length), and L_{STD} equals the fish standard length. Thus, to arrive at a value for swimbladder volume V_{SB} in the original arithmetic scale of measurement, the standard length is substituted for L_{STD} and the calculations specified by the equation are performed to give a value for log (V_{SB} + 1). One subtracted from the antilog of this figure will then furnish an estimate of the swimbladder volume. To obtain any swimbladder volume directly in cubic millimeters, the above equation can be converted to

$$V_{SB}\left[mm^3\right] = (10^a \cdot 10^{bL_{STD}}) - 1 . \tag{3}$$

As in table 2, an asterisk preceeding a regression equation indicates that an F test has shown the slope of the line to be not significant from zero at the 0.05 level of probability. The correlation coefficients R, on the whole, are similar in value to those in the previous analyses (table 2) and exceed 0.70 in 32 of the 55 species.

It is reasonable to assume that the correlations would improve with use of a larger sample size (low R values were associated with 8 species where measurements of 10 or fewer individuals were available), or, perhaps, a more elaborate transformation function. The slope of the regression line at the 0.05 level was shown to be insignificant from zero for 14 of the 55 species. Eight of these were associated with sample sizes of 10 or less. In those species for which a significant slope is indicated, all were positive, with the exception of Lampanyctus cuprarius, which exhibited a slight decrease in bladder volume with increasing fish standard length.

Evidence for the validity of this transformation and regression analysis can be gained by comparing swimbladder volume regression lines from this analysis with individual volumes calculated from the regressions of bladder length and width against standard length. Twelve species, representing in composite a wide range in characteristics, were chosen for this comparison. The 12 species were included because:

1. they contain the four species used previously to demonstrate the curvilinear relation between the raw volumes and standard length (viz., Bonapartia pedaliotia, Lampanyctus festivus, Melamphaes typhlops, and Sternoptyx diaphana);

2. the slope of the regression line has been shown insignificant in three species (viz., Cubiceps spp., Diaphus mollis, and Pollichtys mauli);

3. for those species where a significant slope has been shown to occur, the slopes of the regression lines increase from a low angle (Lampadena urophaos) to a sharp angle (Sternoptyx diaphana);

4. a wide range in standard lengths occurs for Lampadena urophaos and Melamphaes typhlops;

5. a narrow range in standard length occurs for Diogenichthys atlanticus and Melamphaes pumilus;

6. a reasonably large sample size is represented by Lampanyctus festivus (N = 37), Lobianchia gemellari (N = 42), and Melamphaes pumilus (N = 59);

7. a small sample size is shown for Cubiceps spp. (N = 6); and finally

8. correlation coefficients are high (above 0.70) for eight species, intermediate (0.30 - 0.69) for two species, and low (0.16 and 0.21) for two species.

Figure 2A-L presents plots of the transformed swimbladder volumes log (V_{SB} + 1) against fish standard length (shown as open circles) for the 12 selected species. Swimbladder volumes may be read directly from the equivalent scale shown on the axis on the right side of each figure. Superimposed on each graph is the line of best fit specified for each species by the regression equations listed in table 4 and the 95-percent confidence limits for each line. Bladder volumes were also calculated using equation (1), where the values for bladder length and width for a given species of given standard length were determined from the regression equations given in table 2. The quantity one was added to each of these calculated bladder volumes; the logarithms of these sums are shown on each graph as closed circles spaced at more or less regular intervals of standard length along each regression line.

With the exception of Lobianchia gemellari and perhaps Melamphaes typhlops, the bladder volumes estimated by these two separate methods show remarkably close agreement within the limits of the data used to construct the regression line.

In several species, notably Cubiceps spp., Lampanyctus festivus, Bolinichthys indicus, Melamphaes typhlops, and Sternoptyx diaphana, swim-

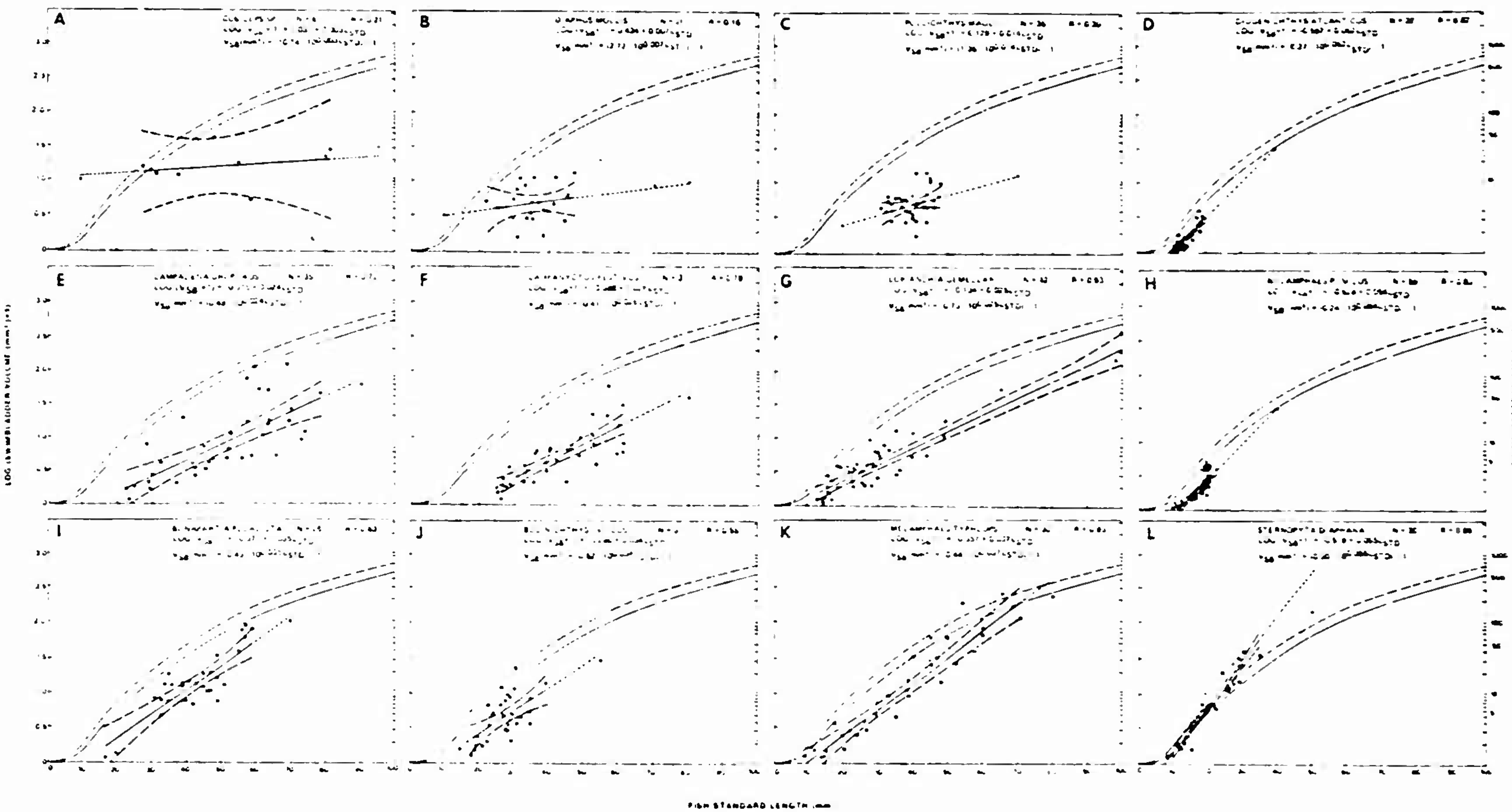

Figure 2. Swimbladder Volume Regression Lines Compared With Individual Volumes Calculated From Regressions of Bladder Length and Width Against Fish Standard Length and With Regression Lines From Previous Work

bladder volumes estimated by the two methods diverge to varying degrees when the uppermost limit of standard length included in the bladder volume regressions is exceeded by 15-20 mm (dashed lines). In other species, namely, Diaphus mollis, Pollichthys mauli, Diogenichthys atlanticus, and Melamphaes pumilus, little if any digression is present within these same limits. Poorest agreement between the two methods occurs for the species Lobianchia gemellari. Because the relationship between fish standard length and bladder dimensions is linear, extrapolation of the regression lines relating these variables beyond the actual data will probably furnish a good approximation of what occurs in the population. Bladder volumes can then be calculated by using equation (1) for specimens outside the limits of the measurement data included in the present analyses.

On the other hand, since the relationship between standard length and bladder volume is curvilinear, estimation of bladder volumes by extrapolation is cautioned against as inappropriate. The two curves drawn with tone on each graph are the solutions to equations derived by Andreeva and Chindonova (upper toned curve) and by Haslett (lower toned curve); they will be given and discussed below.

INTRA- AND INTER-SPECIFIC SWIMBLADDER VARIABILITY

As can be seen from the plots in figure 2A-L, the volume of the swimbladder of a particular fish species of given standard length can vary greatly. In the case of Bonapartia pedaliota (figure 2I), three separate fish with a standard length of 49.0 mm had calculated bladder volumes of 6.5, 15.7, and 32.8 mm^3, and even greater potential variability is shown for Lampadena urophaos (figure 2E). The variability in bladder volume is considerably less, however, in Sternoptyx diaphana (figure 2L) and Diogenichthys atlanticus (figure 2D).

A visual comparison of the regression lines relating bladder volume to fish standard length in different species of the same genus reveals wide differences in the slopes and elevations of these lines. Figure 3A illustrates these differences for five species belonging to the genus Diaphus. The number in parenthesis after each specific name gives the sample size. Next is the correlation coefficient; asterisks indicate that the F test showed that the slope was not significantly different from zero. The range in fish standard length on which each analysis is based is indicated by the limits of the regression line for each species. The slope and elevation of the lines for Diaphus metapoclampus and D. rafinesquei are similar, but they differ markedly from those of the other three species of this genus.

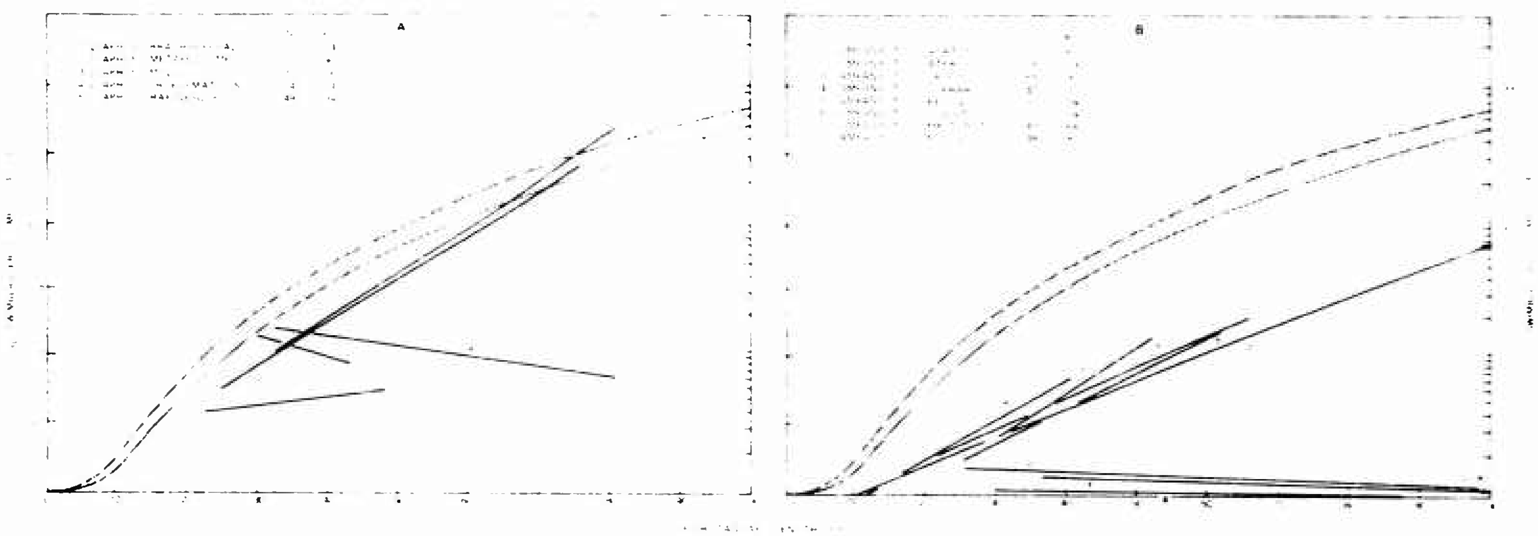

Figure 3. A Comparison of the Slopes and Elevations of Regression Lines Relating Swimbladder Volume to Fish Standard Length for 13 Species Of 2 Genera of Midwater Fishes

Figure 3B presents a similar comparison for eight species of the genus Lampanyctus. As in the former genus, species of Lampanyctus appear to separate into two more or less distinct groups: one, in which bladder volumes are small and change little with increasing standard length (Lampanyctus ater, L. cuprarius, and L. lineatus); and the other, where the rate of increase in bladder volume with increasing standard length is similar for the five remaining species.

Clearly, swimbladder volumes relative to fish standard length of these fish are highly variable within a given species, between species of the same genus, and between different genera of the same family. These results agree with findings of Capen (1967), Shearer (1970), and Kleckner and Gibbs (1972); they also report wide inter- and intra-specific variability in bladder volume. According to Kleckner and Gibbs (ibid., p. 237), much of this variability may be due to an ability of some (perhaps all) species of the Myctophidae to contract the bladder within the covering layer of peritoneum. The authors go on to point out that some of the variability in bladder volume within a given species occurs "where both contracted and inflated bladders may be present at all sizes or may be size dependent." Conversely, the ability to contract the bladder was not observed in specimens belonging to the Gonostomatidae or Sternoptychidae (ibid., p. 247).

Some of the regressions shown in figures 3A and B indicate a close similarity in slope and elevation, for example, between Diaphus metapoclampus and D. rafinesquei, between Lampanyctus festivus and L. photonotus, and between L. ater, L. lineatus, and L. cuprarius. To verify these apparent similarities between regressions, a T test described by Snedecor (1956, p. 178) was used to test the hypothesis that samples of R for the respective species were drawn from a common population correlation. The test showed that the regressions for each of the species combinations mentioned above, in fact, did not differ significantly at the 0.05 level of probability. In addition, the test showed that the correlation coefficients for Diaphus metapoclampus and D. rafinesquei differed significantly from those of D. brachycephalus, D. mollis, and D. problematicus. The same test showed that the respective correlation coefficients for Lampanyctus festivus and L. photonotus and again for L. ater, L. lineatus, and L. cuprarius were drawn from a common population correlation, respectively, but that there was a significant difference (0.05 level) between these two species groupings.

Because swimbladders presumably influence the vertical distribution and migration of midwater fish, it would be interesting to learn if the similarities/differences in the slopes and elevations of the regressions for the above-

mentioned groups of species could be matched with some aspect of fish vertical distribution/migration of functional significance. Bone (1973) suggested that, in certain myctophids, functional types can be grouped by swimbladder state, lipid content, density, and size of pectoral fins. Unfortunately, none of these seven species was collected in large enough quantity in discrete-depth samples to permit formulating now any conclusions about this aspect of swimbladder development.

When adequate additional measurements of standard length and bladder volume become available, a definitive assessment might be provided by using covariance analysis. Application of such a technique would provide a more objective comparison of the regression lines for species included in this study and would, within predetermined probability levels, specify the species whose regressions of bladder volume against standard length exhibited affinities with other species. A more critical evaluation of the functional significance of these relationships could then be undertaken.

SWIMBLADDER FORMATION AND FISH STANDARD LENGTH

The point at which a regression line intercepts the x or y axis often furnishes some clue to the early development of biological populations when experimental or empirical data are lacking. According to Marshall (1960), the teleost swimbladder develops early, although there is uncertainty as to when or how the bladder becomes filled with air (thereby beginning its use as a hydrostatic organ). He points out that large subdermal spaces in the larvae of myctophid species, which develop a well-formed adult swimbladder, may assist in bringing the specific gravity of the larva closer to that of its environment. In ceratioids, where no trace of a swimbladder is found in either the larvae or adults, Bertelsen (1951) hypothesises that gelatinous tissue under the larval skin may serve as a buoyant device.

Here, the x-axis intercept of the regressions of bladder volume against standard length for selected species was examined to obtain an estimate for the mean standard length at which the swimbladder in a given species might form. Twenty of the 55 species were selected for this examination, based on the following criteria:

- Sample size greater than 10

- Correlation coefficient of 0.70 or higher

- Calculated bladder volumes approaching zero in the transformed scale for at least a few smaller specimens in each species.

The last requirement assured the inclusion of only those regressions whose lower limit extended to, or close to, the x axis. That reduced or eliminated the need to extrapolate the regression line, a procedure already cautioned against as inappropriate.

The 20 species thus selected are those for which the "best" data are available. Listed in table 5 are their respective sample sizes, correlation coefficients, smallest specimens for which measurements are available, and the estimated mean fish standard length at zero bladder volume. These standard lengths range from 3 to 14 mm with a grand mean of 10 mm. For the most part, these estimates of standard length would be reached during the late larval-early postlarval stage of development.

SWIMBLADDER VOLUME RELATED TO FISH VOLUME AND LENGTH

Jones (1951) calculates that for a marine teleost to achieve neutral buoyancy, the volume of the swimbladder should be somewhat less than 5 percent of the total fish volume. Marshall (1960) and other investigators also feel that the 5-percent ratio is a reasonable figure. On the other hand, more recent measurements of swimbladder dimensions and total fish volume show that the bladder volume of midwater fishes rarely reaches 5 percent of total fish volume (Capen, 1967; Kleckner and Gibbs, 1972). Horn (1975) reports the mean ratio of swimbladder volume to total fish volume for 12 species of stromateoid fish ranged from 0.6 to 3.4 percent. Increasing evidence indicates that lipids play an important role as a buoyancy device in several species of midwater fish (Butler and Pearcy, 1972; Horn, 1975).

Other authors have related swimbladder volume to the more easily measured fish total length and have derived the following formulas:

$$V_{SB} = 3.4 \times 10^{-4}\, L_{TL}^{3} \quad \text{(Haslett, 1962)} \tag{4}$$

$$V_{SB} = 5 \times 10^{-4}\, L_{TL}^{3} \quad \text{(Andreeva and Chindonova, 1964),} \tag{5}$$

where V_{SB} is the swimbladder volume in cm^3 and L_{TL} is the fish total length in cm. Haslett's equation is derived from his studies of six specimens of the

Table 5. Estimated Mean Fish Standard Length at Time of Bladder Formation

Species	Sample Size	Correlation Coefficient R	Smallest Specimen Measured	Estimated Mean Fish Standard Length at Zero Bladder Volume
Argyropelecus aculeatus	30	0.92	9.0	6
Argyropelecus hemigymnus	47	0.97	7.2	8
Benthosema suborbitale	11	0.71	11.6	12
Diaphus rafinesquei	49	0.94	7.4	3
Diogenichthys atlanticus	32	0.82	11.1	11
Hygophum benoiti	70	0.87	6.3	8
Hygophum taaningi	15	0.72	12.4	11
Lampanyctus crocodilus	65	0.97	9.5	10
Lampanyctus pusillus	48	0.87	6.4	11
Lepidophanes gaussi	32	0.82	15.4	14
Lobianchia gemellari	42	0.93	12.8	6
Melamphaes pumilus	59	0.83	10.2	12
Melamphaes typhlops	30	0.93	9.6	10
Myctophum nitidulum	21	0.95	16.3	14
Poromitra capito	32	0.97	12.0	13
Scopeloberyx opisthopterus	30	0.85	13.0	10
Sternoptyx diaphana	30	0.96	8.9	8
Valenciennellus tripunctulatus	71	0.78	11.2	9
Vinciquerria attenuata	44	0.90	12.4	12
Vinciquerria poweriae	34	0.86	12.1	12

whiting, Gadus merlangus, and is based on a mean bladder volume equal to 4.1 percent of total fish volume. According to Andreeva and Chindonova, their equation is "only very approximate" and assumes that

$$\text{fish volume} = 0.01\ L^{3},$$

where L is apparently fish total length in cm and bladder volume equals 5 percent of total fish volume. Shearer (1970), who determined swimbladder volumes for 91 fresh specimens belonging to 4 species of mesopelagic physoclistous fishes essentially by the method of Kanwisher and Ebeling (1957), reported wide discrepancies and little correlation between estimated bladder volumes for 3 of these species and those calculated from total lengths by either equations (4) or (5).

The present report offers additional comparison with results of Andreeva and Chindonova, Haslett, and Shearer. Equations (4) and (5) are expressed in fish total length. To make them compatible with fish standard length used here, they were converted to the equations

$$V_{SB} = 5.2 \times 10^{-4}\ L_{STD}^{\ 3} \tag{6}$$

and

$$V_{SB} = 7.6 \times 10^{-4}\ L_{STD}\ , \tag{7}$$

respectively, by assuming that fish total length L_{TL} is 15 percent greater than fish standard length L_{SL}. The solutions to these equations are plotted as toned curves in figures 2A-L, 3A-B, 4A-C, and 5A-P. These curves in figures 2 and 3 reveal a poor match (for every species except Sternoptyx diaphana) between bladder volumes estimated from the current research and those estimated from either equations (6) or (7).

One may argue, perhaps justifiably, that the correlation coefficients for the regressions of several species (viz., Cubiceps sp., Diaphus mollis, Pollichthys mauli, Bolinichthys indicus, Diaphus brachycephalus, D. problematicus, Lampanyctus alatus, L. ater, L. cuprarius, L. lineatus, and L. photonotus) are low enough to invalidate such a comparison. The fact remains, however, that a poor match still exists, even for species with high (>0.70) correlation coefficients (viz., Lampadena urophaos, Lampanyctus festivus, Lobianchia gemellari,

Bonapartia pedaliota, Melamphaes typhlops, Diogenichthys atlanticus, Melamphaes pumilus, Diaphus metapoclampus, D. rafinesquei, Lampanyctus crocodilus, and L. pusillus). Similar comparisons of Andreeva and Chindonova's and Haslett's curves with other species included in this study, though not shown here, are equally poor.

Figure 4A-C shows a comparison of the regressions of fish length versus bladder volume for three Ocean Acre species (Lepidophanes guentheri (R = 0.97), Myctophum nitidulum (R = 0.95), and Sternoptyx diaphana (R = 0.96)) with regressions presented by Shearer (1970) for these same species. No comparison was made with Shearer's fourth species, Diaphus brachycephalus, because of the low correlation coefficient (R = 0.14) associated with the Ocean Acre data. The original equations given by Shearer for the regressions for Lepidophanes guentheri (R = 0.46), Myctophum nitidulum (R = 0.53), and Sternoptyx diaphana (R = 0.88) are

$$V_{SB} = 0.98\ L_{TL}^{2.53}, \tag{8}$$

$$V_{SB} = 2.81\ L_{TL}^{1.95}, \tag{9}$$

and

$$V_{SB} = 1.52\ L_{TL}^{2.63}, \tag{10}$$

respectively, where L is total length in cm and V_{SB} is swimbladder volume in mm^3. These have been converted to make them compatible as follows:

$$V_{SB} = 0.004\ L_{STD}^{2.53} \text{ for Lepidophanes guentheri} \tag{11}$$

$$V_{SB} = 0.04\ L_{STD}^{1.95} \text{ for Myctophum nitidulum} \tag{12}$$

and

$$V_{SB} = 0.005\ L_{STD}^{2.63} \text{ for Sternoptyx diaphana}, \tag{13}$$

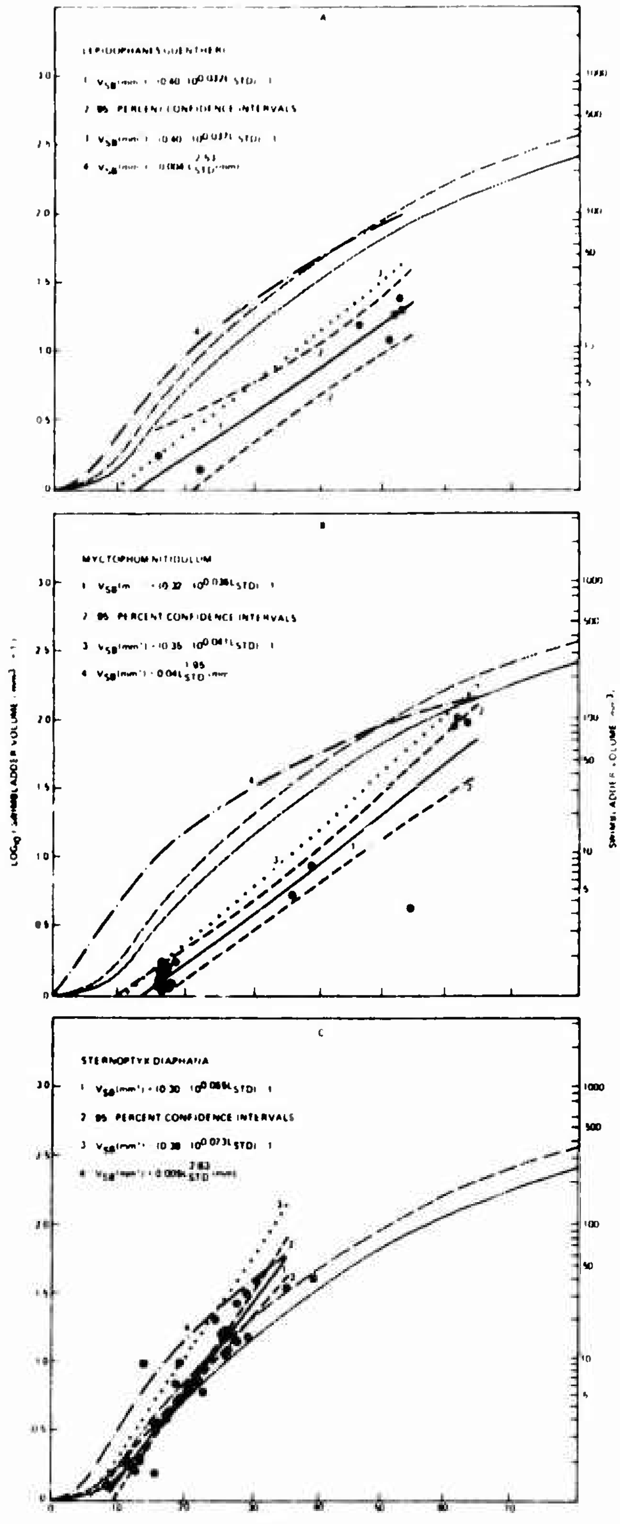

Figure 4. Bladder Volume Regressions of Ocean Acre Fishes Compared With Regressions From the Equations of Shearer, Andreeva and Chindonova, and Haslett Including Calculated Volumes for Marshall's Specimens

where L_{STD} is standard length in mm, V_{SB} is swimbladder volume in mm^3, and it is assumed that

$$L_{TL} = 1.15\ L_{STD}. \tag{14}$$

Bladder volumes estimated by the two methods differ widely, with Shearer's estimates being larger in all three cases. As mentioned above, Shearer worked with fresh material; he determined volume by the method of Kanwisher and Ebeling (1957). According to Andreeva (1964), the linear dimensions of the swimbladders of living fish may be 30 to 40 percent greater than measurements of specimens fixed in formalin. On the other hand, in a recent study of the histology and morphology of stromateoid swimbladders, Horn (1975) allowed only 10 percent for shrinkage of preserved swimbladders. It seems likely that 30 percent represents a maximum value for shrinkage allowance. In the following section, this correction is applied to Ocean Acre swimbladder dimensions. The dotted lines on figure 4 show the effect on the regression line for bladder volume of a 30-percent increase in the linear dimensions of the swimbladder. Although such an increase in linear dimensions yields an increase in bladder volume of almost 120 percent, Shearer's volume estimates are mostly still considerably higher than those determined for Ocean Acre specimens. When Shearer's results are compared with the toned curves shown in figure 4, it can be seen that his estimate of bladder volume for Lepidophanes guentheri agrees fairly well with Andreeva and Chindonova's and with Haslett's estimates but, for the most part, exceeds these estimates for Myctophum nitidulum and Sternoptyx diaphana.

Marshall (1951, 1960) has reported measurements of standard length and bladder dimensions for several species of midwater fish. Wherever his species are common with the species used here, bladder volumes have been calculated from his bladder dimensions with equation (1). These volumes are compared with Shearer's results in figure 4A and C and with bladder volumes resulting from the present study in figure 5A-P. In these figures, Marshall's volume estimates are shown as squares; bladder volumes for Ocean Acre specimens are shown as circles. The least-squares regression line (solid straight line) is shown for each Ocean Acre species, as are the 95-percent confidence intervals (curved dashed lines) around the regression line.

In four species (Lepidophanes guentheri (figure 5A), Benthosema suborbitale (figure 5B), Hygophum benoiti (figure 5C), and Notolychnus valdiviae (figure 5D)), bladder volumes calculated from Marshall's data fall within the 95-percent confidence intervals around the least-squares line calculated for Ocean

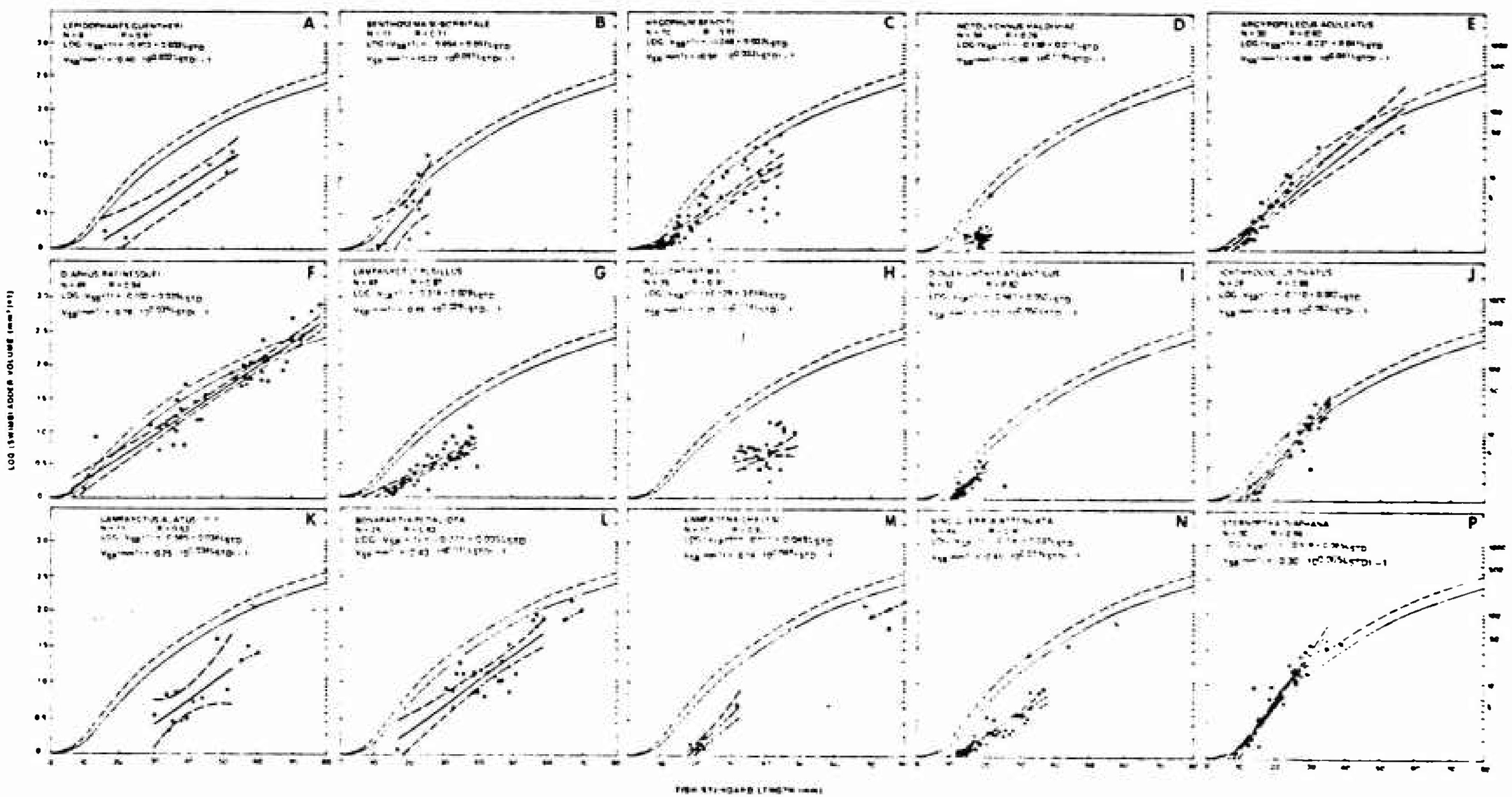

Figure 3. Bladder Volume Regressions of Ocean Acre Fishes Compared With Calculated Volumes for Marshall's Specimens As Well As Andreeva and Chindonova's and Haslett's Regressions

Acre specimens. The bladder volume of Marshall's specimen of Lepidophanes guentheri is considerably less than Shearer's estimate (figure 4A). In four other species (Argyropelecus aculeatus (figure 5E), Diaphus rafinesquei (figure 5F), Lampanyctus pusillus (figure 5G), and Pollichthys mauli (figure 5H)), Marshall's swimbladder volumes fall within the range but outside the confidence limits of volumes one may expect to encounter in Ocean Acre specimens.

In two species (Diogenichthys atlanticus (figure 5I) and Ichthyococcus ovatus (figure 5J)), Marshall's data show bladder volumes considerably smaller than those calculated from Ocean Acre material. The standard lengths of Marshall's specimens of Lampanyctus alatus (figure 5K), Bonapartia pedaliota (figure 5L), and Lampadena chavesi (figure 5M) exceed those of Ocean Acre specimens included here. They cannot be compared with an extrapolated least-squares line for these species. Instead, the regressions for bladder length and width have been used to estimate the bladder volume for Ocean Acre individuals comparable in size to Marshall's specimens. These volumes are shown in figures 5K-M as symbols connected with a dashed line. When compared with bladder volumes calculated in this manner, the volumes of Marshall's specimens of Lampanyctus alatus and Bonapartia pedaliota are somewhat greater. The bladder volume of Marshall's specimen of Lampadena chavesi (figure 5M) is less.

In figure 5N, one of Marshall's three specimens of Vinciquerria attenuata (standard length 22.5 mm) had a calculated bladder volume that fell within the data for Ocean Acre individuals of this species, but two other specimens had bladder volumes that greatly exceeded what might be expected for Ocean Acre specimens.

One final comparison is shown in figure 5P, where volumes of both of Marshall's specimens of Sternoptyx diaphana were outside the range of those calculated for Ocean Acre specimens. As figure 4C shows, the bladder volume of one of Marshall's specimens of Sternoptyx diaphana exceeded Shearer's estimate and the other was less.

Examination of the toned curves in figure 5A-P reveals that in every species (except Sternoptyx diaphana and possibly Argyropelecus aculeatus) swimbladder volumes estimated by equations (6) and (7) exceed volumes estimated for Ocean Acre specimens.

EQUIVALENT RADII AS A PERCENTAGE OF FISH STANDARD LENGTH

Consistent with standard acoustical treatment, we convert swimbladder volumes to radii of spherical bubbles of equal volume. The radii can be used in

the equations for scattering strength (Strasberg, 1953). To the acoustician, then, perhaps the ratio of equivalent radii to fish standard length would be a more directly applicable expression than the ratio of bladder volume to total fish volume. This is especially true since, in most studies of midwater fish, it is conventional to report measurements of fish standard length, but rarely is total fish length reported.

This more applicable ratio is examined for 20 species listed in table 6. The listing (same species as in table 5) includes only those species for which the "best" data are available (i.e., high R values and large sample size). The minimum, maximum, and mean standard lengths listed for each species were used in the regression equation shown for that species in table 4 to calculate bladder volume. These volumes were then converted to their respective equivalent radii and are listed in the appropriate columns of table 6. Where substituting in the regression equation of the minimum standard length yielded a negative value for bladder volume, corresponding equivalent radii are omitted from the table. The last three columns list calculated equivalent radii as a percentage of minimum, maximum, and mean standard length.

The overall average ratio for equivalent radii as a percentage of minimum standard length is shown to be 3.0 percent with a standard deviation of 1.4. For maximum standard length, the average is 4.2 percent with a standard deviation of 1.1, and for the mean standard length, 3.5 percent $\pm$ 0.8. These ratios are lower than the overall ratio of 4.7 percent reported elsewhere.

Results of a student's T test (Snedecor, 1956) indicate that no significant difference exists between the overall average ratio for minimum and mean standard length, but there is (1) a significant difference between the ratios for mean standard length and maximum standard length and (2) between minimum and maximum standard length. This implies that, on the average, swimbladder volume increases relative to standard length (or total fish volume) as fish continue to grow. The reader should note, however, as shown previously, that individual species vary in this respect and may not strictly conform to this average relationship. In principle, this nonconformity agrees with Kleckner and Gibbs' work (1972). They reported that their data on bladder volume and fish length of Mediterranean specimens indicate that, for certain species, the maximum percentage volume of the swimbladder is reached at an intermediate fish length. In other species, bladder volume appears to increase continuously with fish length. For one species, the percentage volume may remain relatively constant with increasing fish length.

Table 6. Ratio of Swimbladder Equivalent Spherical Radii to Fish Standard Length

Species	Sample Size	Range of Standard Lengths	Mean Standard Length	Equiv. Radii of Swimbladder Volume			Equiv. Radii as Percent of Standard Length		
				Min STD L	Max STD L	Mean STD L	Min STD L	Max STD L	Mean STD L
Argyropelecus aculeatus	30	9.0-55.9	17.1	0.45	3.01	0.78	5.0	5.4	4.6
Argyropelecus hemigymnus	47	7.2-33.8	20.1	----	1.78	0.94	---	5.3	4.7
Benthosema subrobitale	11	11.6-26.0	20.4	0.16	1.11	0.81	1.4	4.3	4.0
Diaphus rafinesquei	49	7.4-77.6	50.0	0.47	4.61	2.16	6.4	5.9	4.4
Diogenichthys atlanticus	32	11.1-19.4	14.3	0.18	0.75	0.49	1.6	3.9	3.4
Hygophum benoiti	70	6.3-44.0	20.8	----	1.53	0.75	---	3.5	3.6
Hygophum taaningi	15	12.4-39.8	22.5	0.28	1.06	0.63	2.3	2.7	2.8
Lampanyctus crocodilus	65	9.5-171.7	56.1	0.21	8.59	1.29	2.2	5.0	2.3
Lampanyctus pusillus	43	6.4-40.0	27.3	----	1.13	0.78	---	2.8	2.9
Lepidophanes gaussi	32	15.4-41.9	28.6	0.31	1.27	0.81	2.0	3.0	2.8
Lobianchia gemellari	42	12.8-39.8	29.7	0.50	3.79	0.90	3.9	3.8	3.0
Melamphaes pumilus	59	10.2-21.4	17.6	----	0.83	0.65	---	3.9	3.7
Melamphaes typhlops	30	9.6-70.8	36.5	----	3.52	1.28	---	5.0	3.5
Myctophum nitidulum	21	16.3-63.6	27.5	0.39	2.45	0.80	2.4	3.9	2.9
Poromitra capito	32	12.0-99.1	35.6	----	5.21	1.03	---	5.3	2.9
Scopeloberyx opisthopterus	30	13.0-38.6	27.[illegible]	0.39	1.34	0.94	3.0	3.5	3.4
Sternoptyx diaphana	30	8.9-35.0	20.6	0.33	2.37	1.10	3.7	6.8	5.3
Valenciennellus tripunctulatus	71	11.2-29.5	21.[illegible]	0.41	1.31	0.93	3.7	4.4	4.2
Vinciquerria attenuata	44	12.4-36.4	20.3	0.22	1.09	0.60	1.8	3.0	3.0
Vinciquerria poweriae	34	12.1-33.7	20.6	0.26	1.01	0.62	2.1	3.0	3.0
					AVERAGE		3.0±1.4	4.2±1.1	3.5±0.8

SUMMARY AND CONCLUSIONS

This report examines the relationship of fish standard length to swimbladder dimensions; the intra- and inter-specific variation is also measured in over 1600 selected midwater fish specimens belonging to 55 species from 9 families. These species are believed to account for most acoustic volume reverberation occurring throughout a large part of the Sargasso Sea.

It is shown that fish standard length is linearly related to swimbladder length and swimbladder width. Linear regression equations are presented to define these relationships.

The relationship of fish standard length to swimbladder volume is shown to be of exponential form. To facilitate analyzing this relationship a logarithmic transformation commonly employed in fisheries work is applied to the bladder volume data, and additional regression equations are presented to relate fish length to bladder volume. The slopes of these regression lines are shown to be insignificant from zero for 14 of the 55 species. For the remaining 41 species, all slopes were positive (with the exception of Lampanyctus cuprarius, which showed a slight decrease in bladder volume with increasing fish standard length).

The volume of the swimbladder of a given species of given standard length can vary greatly. Three separate specimens of Bonapartia pedaliota, each with a standard length of 49 mm, had calculated bladder volumes of 6.5, 15.7, and 32.8 mm^3. In other species, such as Sternoptyx diaphana and Diogenichthys atlanticus, variability in bladder volume was considerably less. Comparison of the elevations and slopes of regression lines for different fish species also reveals wide differences.

From considerations of the x-axis intercept of the regression lines relating fish standard length to swimbladder volume, it is suggested that the actual formation of the swimbladder may occur during the late larval-early postlarval stage of development in the 20 mesopelagic fish species examined.

Swimbladder volumes estimated from this study are in fair agreement with the measurements published by Marshall (1951, 1960) for like species of fish but, for the most part, are considerably less than volumes estimated by either Haslett's (1962), Andreeva and Chindonova's (1964), or Shearer's (1970) equations.

The overall mean ratio for swimbladder equivalent spherical radii as a percentage of fish minimum, maximum, and mean standard lengths are 3.0, 4.2, and 3.5 percent, respectively. These ratios suggest that, on the average, swimbladder volume increases relative to standard length as fish continue to grow.

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